Discussion

Sphaerodactylus copei has been shown to be divisible into four very distinct races on the basis of coloration, head pattern, and scalation. The species is known to occur only on the Tiburon Peninsula in southwestern Hispaniola, and presently is unknown from the affiliated Península de Barahona in the República Dominicana. *S. copei* is thus completely restricted to the south island and does not occur in, or even closely approach, the Cul-de-Sac plain. In actuality the species appears to be absent from the higher mountains in the Massif de la Selle and Massif de la Hotte; thus the northern (*copei* and *picturatus*) populations are effectively isolated from the southern (*enochrus* and *cataplexis*) populations, except that apparently *cataplexis* has crossed the mountains in the Fond-des-Nègres region and occurs on the north coast as well, between the ranges of *copei* and *picturatus*. Both *picturatus* and *cataplexis* have insular populations, the former on Grande Cayamite, the latter on Ile-à-Vache, which have not differentiated from the populations on the (more or less) adjacent mainland.

Only two species of *Sphaerodactylus* are known from the Tiburon Peninsula: *S. copei* and *S. cinereus*, although Cochran (1941, p. 112) listed a specimen of *S. stejnegeri*, collected by W. L. Abbott in "southwestern Haiti". During the period of 1917-18, Abbott did indeed collect extensively on the Tiburon Peninsula near Jérémie, Moron, and Moline, but between March 5 and 12, 1918, he collected near Etang Saumatre and Trou Caiman, (see Wetmore and Swales, 1931:25-26) both localities in the Cul-de-Sac whence *S. stejnegeri* is known. It is thus not unlikely that *S. stejnegeri*, typically a xeric region lizard, does not occur on the Tiburon Peninsula. Neither of these species (and in fact, no *Sphaerodactylus*) has been reported from the adjacent Ile de la Gonave, an island whose fauna shows some distinct relationships with that of the Tiburon Peninsula. Apparently *S. copei* has evolved on the western two thirds of the south island, has differentiated both on the north and south sides of the central mountain massifs, and has been able to cross these ranges at least in the relatively low Fond-des-Nègres area. It would not be surprising if *S. copei* were to be taken in the region of the Vallée de Trouin; specimens from this area may well be found to be intergrades between the races *copei* and *enochrus*.

At least in our experience, *S. copei* is distinctly not a gecko of xeric situations. At Camp Perrin they were extremely abundant,

occurring under almost any ground cover, and in piles of rocks and in old stone walls. At Diquini a small series was taken under rocks on the floor of the well-known cave at that locality. Camp Perrin lies at an elevation of about 1000 feet and, although not extremely wet, is certainly mesic and presumably was once forested. The Diquini area likewise is moderately mesic, with lowland cut-over forest adjacent to the cave. The altitudinal distribution of S. *copei* varies from sea level (Ça Ira, Ile-à-Vache, Les Cayes) to 1000 feet (Camp Perrin); it is possible that some of the unlocatable Miragoâne localities may be slightly higher than Camp Perrin.

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ISOLATING MECHANISMS IN SNAKES

Wilfred T. Neill

Mechanisms bringing about reproductive isolation have often been investigated in frogs (Mecham, 1961), but not in other herpetozoan groups. In the current state of knowledge it would be impossible to generalize about isolating mechanisms in the salamanders, turtles, or lizards. The present paper summarizes the mechanisms that are thought to exist among snakes. The summary is based largely upon personal observation in field and laboratory, supplemented by a review of the literature. The bibliographic references are not intended to be exhaustive. Where possible, common names as well as scientific ones are employed, to render the account more meaningful to the non-herpetologist.

The study is concerned primarily with mechanisms that operate at the species level; that bring about the reproductive isolation of two closely related, usually congeneric, species.

Account of Mechanisms

1. The most obvious form of reproductive isolation is geographic. Two species, however compatible otherwise, will not interbreed in nature if their respective ranges are not in contact.

Congeners are often allopatric in snakes, but this need not be the case. For example, the snake fauna of Alachua County, Florida, includes five monospecific genera (*Cemophora, Drymarchon, Liodytes, Seminatrix, Stilosoma*); two genera each with two species in the county, and no additional species in other areas (*Farancia, Virginia*); seven genera each with only one species in the county, but with one or more additional species elsewhere (*Agkistrodon, Diadophis, Micrurus, Opheodrys, Pituophis, Sistrurus, Urotheca*); eight genera each with two species in the county, and with one or more additional species elsewhere (*Coluber, Crotalus, Elaphe, Heterodon, Lampropeltis, Storeria, Tantilla, Thamnophis*); and one genus with five species in the county and additional species elsewhere (*Natrix*).

Range maps for North American snakes (Wright and Wright, 1957) show both allopatry and sympatry among congeners.

2. Two congeneric snakes may be sympatric, but confined to different habitats and therefore unlikely to interbreed.

Thus, in Marion County, Florida, the mud snake (*Farancia abacura*) inhabits acidic ponds, bogs, and swamp streams, while the rainbow snake (*F. erytrogramma*) inhabits basic (calcareous) spring runs (Neill, 1964, pp. 272-274, fig. 5). In Richmond County, Georgia, the cottonmouth (*Agkistrodon piscivorus*) is aquatic and riparian, while the copperhead (*A. contortrix*) is terrestrial on higher ground bordering stream valleys. In the Florida Panhandle, the glossy watersnake (*Natrix rigida rigida*) is confined to ponds, while the queen snake (*N. septemvittata septemvittata*), a near ally, is confined to streams. Throughout their area of sympatry in Georgia and Florida, the coachwhip (*Coluber flagellum*) inhabits the drier situations, the blacksnake (*C. constrictor*) the damper ones. Many other examples could be listed.

But it is seldom that two sympatric, congeneric snakes are so divergent in habitat that they cannot occur together in some intermediate situation. I have collected the mud snake and rainbow snake together in large, spring-fed streams with swampy borders and tributaries; the cottonmouth and copperhead under the same bridge; the coachwhip and blacksnake in wiregrass flatwoods (*Pinus-Aristida* community), which vary from very wet to very dry. In some cases, two closely related species occur very commonly in the same habitat. Thus the red-bellied watersnake (*Natrix erythrogaster erythrogaster*) and the banded watersnake (*N. fasciata fasciata*) are found together in and beside lakes, ponds, swamps, and streams in the Atlantic Coastal Plain of Georgia.

Carr (1940) described the respective habitats of Florida snakes.

3. Two sympatric, congeneric snakes may occupy the same habitat, yet fail to interbreed because they seek different microhabitats during the mating season.

Thus, as noted, the red-bellied watersnake and the banded watersnake occur together in aquatic and riparian situations of the Atlantic Coastal Plain in Georgia; but in that region the former always mates in shallow water, while the latter always leaves the water to mate. Mating pairs of the banded watersnake are often found as much as 30 to 40 feet back from the water, where individuals of the species are not otherwise to be expected.

A slightly different situation involves the brown watersnake (*Natrix taxispilota taxispilota*). In the Atlantic Coastal Plain of Georgia it is confined to larger streams and lakes, where it is associated with the red-bellied and banded watersnakes. All three

species commonly bask on tree limbs overhanging the water; but the brown watersnake, unlike the other two, also mates in this arboreal milieu. Arboreal mating has been reported for the brown watersnake in Florida as well (Carr, 1940, p. 89).

Separation by mating microhabitat is fairly common among snakes, but has not previously been discussed in the literature.

4. Two sympatric, congeneric snakes, occupying the same habitat, may be prevented from interbreeding by the timing of their respective reproductive cycles.

In Richmond County, Georgia, the blacksnake is the first snake to emerge from hibernation in the spring, appearing as early as latter February and mating soon after. But in the same region, the coachwhip is the last species to emerge, rarely appearing before April, by which time the blacksnake has finished mating.

The isolation of sympatric, congeneric snakes, through interspecific differences in mating season, has been observed for several genera of the Southeast, but has not been discussed in the literature. Fox (1954) investigated the proximate causes of interspecific differences in the timing of the reproductive cycle among certain California gartersnakes (*Thamnophis*). Neill (1962) summarized observations on the ultimate causes of the ophidian reproductive cycle.

5. Certain aspects of ophidian courtship behavior function to discourage interspecific mating.

Many accounts of supposed courtship in snakes (Davis, 1936) are now known to relate actually to the "combat dance" of two males (Shaw, 1951); but some snakes do perform fairly elaborate courtship antics (Noble, 1937). The true courtship has been studied in only a minority of snake species, and further work may reveal some exceptions to the following generalizations.

The male snake is the more active in courtship, seeking out the female. The courting male is especially stimulated to follow the scent trail of an oestrous female of his own species (Noble, 1937; Noble and Clausen, 1936). Commonly, several males find and try to mate with one female (Finneran, 1949). The female is apt to reject the first few advances; she dashes away, the males pursuing. Having overtaken the female, the courting male rubs his chin along her back, while repeatedly flickering his tongue in and out. Finally his chin is appressed to her nuchal region. Usually the male makes very sharp twitching or jerking motions, and

undulant body movements that begin caudally; there is some intertwining or overlapping of bodies, and the male lifts the female's cloacal region to permit intromission.

In some species the undulant body movements are lacking and the male bites the female along the body, especially in the nuchal region. In the blacksnake, both sexes dash about before settling down to the Liebesspiel (Noble, 1937).

Courtship may continue for days before the female is aroused to the point of acceptance. In one case a captive male red-bellied watersnake courted almost continuously for a month without arousing the female (Carr, 1940, p. 89). Repeated rejection of a male may often reflect the circumstance that the female has not become physiologically or psychologically ready for mating. However, this need not always be the case; a female may reject one male only to accept another (Munro, 1948).

In captivity, enforced proximity with other species could encourage an abnormal amount of attempted cross-mating; but on the other hand, debilitating or highly unnatural cage conditions could inhibit mating activity of any kind. In my experience, a healthy male snake, if well adjusted to captivity, if exposed to some natural fluctuations of temperature and illumination, and if deprived of a normal mating outlet, will attempt a cross-mating with a congener, or even with a distantly allied species, during the male's normal mating season. However, certain species are far more persistent in their cross-mating efforts than are others. Probably the least discriminating is the eastern hognose snake (*Heterodon platyrhinos*); captive males of this species will attempt to mate with almost any kind of snake, of either sex.

Male gartersnakes, courting their own kind, ignored anesthetized or freshly killed females (Noble, 1937); but male hognose snakes attempted to mate with a dead female of their own kind (Medsger, 1927), and a male lancehead snake (*Bothrops jararaca*) attempted a necrophilous intergeneric mating (Amaral, 1932).

A minority of snake species are provided with special anatomical structures that function during courtship and mating. Chin tubercles, which hypertrophy during the mating season, may serve a hedonic function (Blanchard, 1931). Supracloacal tubercles serve a tactile function (Blanchard, 1931; Noble, 1937). The hind limb vestiges of certain boas (Boidae) are used by the male to scratch

or stroke the female during courtship, and also function as claspers (Davis, 1936).

Sexual dimorphism in color has been reported for about a dozen species of snakes (Neill, 1964, p. 282), but its possible role in courtship is unknown.

Of the various aspects of ophidian courtship, three closely interrelated ones seem especially important in preventing a cross-mating. One is the tendency for the male to follow the scent trail of an oestrous female of its own species. A second is the inclination of the female to withdraw when first approached by a courting male, and to accept a male only after some pursuit. A third factor is the considerable length of time necessary for a courting male to arouse the female to the point of acceptance. Presumably, a courting male would not trail a female of another species with as great a persistence as he would a female of his own species; and the longer the interspecific courtship, the greater the likelihood that the male will be eluded by the coy female, or will undergo a weakening of the trailing impulse, or will be diverted onto a trail of his own kind.

6. A difference in size may function in three ways to prevent the interbreeding of congeneric snakes.

A scarlet kingsnake (*Lampropeltis d. doliata*), usually under 45 cm. in total length, probably could not mate with a Florida kingsnake (*L. getulus floridana*) even if both individuals were stimulated to attempt the cross-mating; for examples of the latter species commonly exceed 150 cm. in length.

Also, a large snake, simply by virtue of its size, might well evoke from a smaller congener an avoidance reaction taking precedence over reproductive urge.

Finally, many snakes prey upon smaller individuals of other species; and, within certain of the more ophiophagous genera (*e.g., Coluber, Lampropeltis, Agkistrodon*), a large snake might regard a smaller congener as prey rather than as a potential mate.

Among snakes, two sympatric, congeneric species usually differ in both average and maximum size, but the difference is rarely so great as to rule out all possibility of cross-mating. Normal matings commonly involve a small male and a much larger female; for in most snake species, the females average decidedly larger than the males, and reach a greater maximum size.

7. Interbreeding of congeners may be limited by interspecific differences of the reproductive organs.

The hemipenis of the male snake is an extraordinary structure; it is equipped basally with hooks or enlarged spines, and more distally with spines, flounces, calyces, etc., depending on species (Dowling and Savage, 1960). The anatomy of the female's cloaca must be such as to permit reception of the various spines, etc. If the hemipenis of the male is spinous in a given species, the cloaca is thick-walled in the female of that species; if the hemipenis is smooth, the female's cloaca is thin-walled (Cope, 1900, p. 700; Pope, 1941). The copulating male is anchored firmly by the basal spines or hooks of the hemipenis (Beuchelt, 1936); the more distal ornamentation must serve another function.

Hemipenial characters were found to be constant in nineteen species of the snake genus *Calamaria*, but variable in a twentieth (Inger and Marx, 1962). The size of the basal hooks or spines is a character of subspecific import in the blacksnake (Auffenberg, 1955). Hemipenial differences often exist at the specific and generic levels (Dowling and Savage, 1960), and at higher levels (Clark, 1944).

Two Old World species of lancehead snakes (*Trimeresurus*), externally very similar, differ so markedly in hemipenial characters, and correlated cloacal characters of the female, that a cross-mating might be mechanically impossible (Pope, 1941). Such an extreme difference between congeners is, however, unusual; in most cases a male snake, attempting an interspecific mating, probably would not be prevented from intromission by interspecific differences in hemipenial ornamentation.

A small male of the eastern hognose snake (*Heterodon platyrhinos*) mated with a large female of the southern hognose snake (*H. simus*); the female died three days later, possibly from cloacal lacerations produced by the hemipenial spines of the male (Neill, 1951, pp. 52-53, fig. 2).

Pope (1941, as *Liophis*) examined a pair of *Leimadophis poecilogyrus*, preserved and fixed while in copula. The tips of the divided sulcus spermaticus were closely appressed to the openings of the oviducts, and the hemipenial ornamentation gripped the female's cloacal walls so firmly that no shifting from this position was possible. The circumstance suggests the probability that insemination is accomplished more effectively in a normal mating,

with close hemipenial-cloacal correspondence, than in an inter-specific mating without such correspondence.

8. An interspecific mating may prove fruitless, or relatively so as compared with a normal mating, in consequence of physiological incompatibility. By this is not meant genetic incompatibility, but the failure of the sperm to survive in an alien environment: the reproductive tract of a female snake belonging to another species.

When fertilization immediately or shortly follows mating, this factor may not be important. However, sperm storage is carried on by various snakes (Neill, 1962, pp. 247-248). Indeed, the females of all snakes may be provided with seminal receptacles (Fox and Dessauer, 1962, pp. 595). In one case, a single copulation sufficed for the production of fertile eggs in at least five successive years (Haines, 1940). One would suppose the longevity of sperm to be reduced in an alien seminal receptacle.

Although an ectotherm, a snake, at least during its active season, maintains a fairly constant body temperature by restricting its activity to times when, and places where, certain environmental temperatures prevail; and within this thermal activity range there is an eccritic (*i.e.*, "preferred")temperature (Cowles and Bogert, 1944; Fitch, 1956). The eccritic temperature may differ between congeneric snakes, by a few Centigrade degrees; and the thermal activity range may differ even more markedly. Reptile sperm cells may be adversely affected by a few degrees rise of temperature (Cowles and Burleson, 1945). Little is known of other factors that might conceivably affect sperm longevity in reptiles.

9. If an interspecific mating is accomplished, its effectiveness may be limited by genetic incompatibility.

There were a few early accounts of supposed hybridization between snakes of remotely related genera, such as *Natrix* $\times$ *Liophis* or even *Natrix* $\times$ *Vipera* (Mertens, 1950). This was prior to the discovery of sperm storage in these reptiles. If a female snake, penned for a long while with a male of a different species, chanced to produce offspring, it was mistakenly assumed that the young had to be of hybrid origin. It is significant that some of these early accounts described the supposed hybrids as resembling the mother. There have been authentic instances of cross-copula between fairly remote relatives, *e. g. Bothrops* $\times$ *Crotalus* (Schöt-

tler, 1950) or *Pseustes* × *Spilotes* (Mole, 1924); but these were without issue.

There are a few acceptable accounts of intergeneric hybrids in snakes; but in each case the hybridizing genera are closely related, their recognition as separate entities being more a matter of nomenclatural convenience than of zoology. One intergeneric rattlesnake hybrid, *Sistrurus* × *Crotalus,* is known (Bailey, 1942; Klauber, 1956, p. 208). Possible hybrids of the mud snake and rainbow snake have been reported, but the two species have lately been placed in one genus, *Farancia* (Neill, 1964, p. 263). Noble (1937) credenced Bonnenberger's (1909) account of a *Natrix* × *Thamnophis* hybridization. A *Thamnophis,* courting its own kind, continued courtship when placed with a *Natrix* (Noble, 1937).

Most snake hybridizations have been between congeners. Mertens (1950, 1956) has summarized much of the pertinent literature. Reported combinations include ratsnakes, *Elaphe guttata* × *E. obsoleta;* watersnakes, *Natrix natrix* × *N. maura, N. natrix* × *N. tessellata, N. tessellata* × *N. maura,* and *N. sipedon* × *N. fasciata* (Conant, 1963); gartersnakes, *Thamnophis marcianus* × *T. radix* (Smith, 1946); hognose snakes, *Heterodon platyrhinos* × *H. simus* (Edgren, 1952); vipers, *Vipera aspis* × *V. ammodytes,* and *V. aspis* × *V. berus;* and rattlesnakes, *Crotalus adamanteus* × *C. horridus, C. unicolor* × *C. scutulatus, C. viridis* × *C. ruber,* and *C. viridis* × *C. scutulatus* (Klauber, 1956).

Supposed viper hybrids, *Viper berus* × *V. ammodytes,* have been described, but their identification as such is questioned by some. Two individual snakes, reported as hybrid (*Thamnophis melanogaster* × *T. rufipunctatus; Bothrops cotiara* × *B. jararaca*), were later interpreted in another fashion. A lancehead cross-copula, *Bothrops jararaca* × *B. neuwiedi,* has been observed.

A watersnake hybridization, *Natrix tessellata* × *N. maura,* produced only four young (Klinge, 1925). *N. tessellata* normally lays 5 to 25 eggs, *N. maura* 4 to 20 (Mertens, 1952). A viper hybridization, *Vipera aspis* × *V. ammodytes,* also produced only four young (Schweizer, 1941). *V. aspis* and *V. ammodytes* each normally produces four to 18 young. In both of the above hybridizations, the relatively small number of offspring suggests some hybrid inviability.

A rattlesnake hybridization, *Crotalus viridis* × *C. ruber,* produced nine young, only one of which lived more than a year. This

one, a male, lived more than nine years, but never mated. Apparently its mechanism for sex recognition was somehow reversed, for it attempted to mate with other males, and to carry on the male "combat dance" with females (Klauber, 1956).

Another rattlesnake hybridization, *Crotalus unicolor* $\times$ *C. scutulatus,* produced four young, all of which were raised to maturity. Of these hybrids, the single female eventually mated with one or more of the males, producing five broods. The F_2 snakes proved very delicate; and autopsy revealed some of them to have anatomical defects of the stomach, heart, liver, and reproductive organs (Klauber, 1956).

Yet another rattlesnake hybridization, *Crotalus viridis* $\times$ *C. scutulatus,* produced twelve young, some of which exhibited asymmetric, partially lineate patterns (Klauber, 1956). Such patterns appear to be strongly selected against in nature, possibly because they are linked with behavioral or physiological abnormalities (Neill, 1963, p. 209).

The foregoing observations imply some genetic incompatibility among snakes at the species level, with greater incompatibility at higher levels.

10. Hybrid adaptive inferiority probably exists in snakes.

The most common snake hybridization involves *Elaphe guttata* and one of the peninsular Florida subspecies of *E. obsoleta.* This hybrid combination has been produced in captivity (Lederer, 1950; Mertens, 1950). Natural hybrids between the red ratsnake ("corn snake," *E. guttata guttata*) and the Everglades ratsnake (*E. obsoleta rossalleni*) have been reported (Neill, 1949, p. 10). Such hybrids are now known to be fairly common about certain small towns on or near Lake Okeechobee in southern Florida.

Under natural conditions the Everglades ratsnake inhabits open sawgrass marshes, and also climbs frequently into trees and shrubs. It has a proportionately long tail. Its pattern is usually lineate, occasionally unicolor. A long tail characterizes most arboreal snakes; and a lineate or unicolor pattern is common among snakes that are arboreal, or that live in graminoids.

In contrast, the red ratsnake, while occasionally climbing about tree stumps and bushes, is often subterranean, frequenting mammal burrows; it also prowls on the surface of the ground, usually in wooded areas. It has a proportionately short tail and a blotched pattern. A short tail characterizes the more secretive or subter-

ranean snakes, and a blotched (disruptive) pattern is usual among snakes that are terrestrial in wooded areas.

Thus, the aforesaid interspecific differences, in tail length and pattern, are probably adaptive. The natural hybrids, all apparently of the F_1 generation, exhibit an intermediate tail length; and their pattern includes the blotches of *Elaphe g. guttata* superimposed, in pallid version, upon the stripes of *E. obsoleta rossalleni*. The hybrids are therefore not ideally adapted for the natural habitat of either parent.

It is probably significant that the *Elaphe* hybrids are collected mostly around human settlements, where the activities of man have reduced the number of organisms that prey upon, or compete with, the ratsnakes; and where unnatural environments, such as rodent-infested outbuildings, are frequented by both species of *Elaphe*.

POSSIBLE ADDITIONAL MECHANISMS

Two other isolating mechanisms should be listed separately because under special circumstances they might function to encourage hybridization rather than to prevent it.

In temperate regions many snakes overwinter communally. In the southern United States only small aggregations are usually formed; but in colder regions, hundreds of snakes may inhabit a single den. Thus a den in Utah yielded 930 Great Basin rattlesnakes (*Crotalus viridis*), 632 striped racers (*Coluber taeniatus*), 127 blue racers (*C. constrictor*), and 41 individuals representing four other species (Woodbury, 1951). With the advent of warmer weather the snakes emerge; and, in many species, mating activities begin before the individuals have dispersed from the den.

In the case of the aforesaid den in Utah, the tendency to aggregate would serve as an isolating mechanism as regards the rattlesnake; for an individual in reproductive condition would probably find and mate with a member of its own species near the den. With the racers, however, the aggregation of two congeners would favor hybridization if the usual isolating mechanisms chanced not to function.

A second possible isolating mechanism has not been discussed in the literature. Both published accounts and personal observation reveal that, among captive snakes, most attempted mismatings—interspecific, necrophilous, and homosexual—result from the

activity of a young male, probably in its first season of breeding. Perhaps the threshold of reproductive activity is lower in the young male. However, I have wondered if there might not be a process, roughly comparable to imprinting, whereby the male's reproductive activity is modified by the first reproductive experience. At any rate, some force seems, with age, to direct the reproductive efforts of the male into proper channels, so that older males rarely attempt any but a normal mating.

TABLE 1

Isolating mechanisms in snakes

I.	*Extrinsic*
	1. Geographic Separation
	2. Habitat Separation
	3. Microhabitat Separation at Mating Time
II.	*Intrinsic*
	4. Timing of Reproductive Cycle
	5. Courtship
	6. Size Difference
	7. Incompatibility of Reproductive Organs
	8. Physiological Incompatibility
	9. Genetic Incompatibility
	10. Hybrid Adaptive Inferiority

Mechanisms above the broken line are pre-mating, the others post-mating. Doubtful or occasionally operative mechanisms are omitted.

DISCUSSION

Both geographic and habitat separation need not have evolved solely as isolating mechanisms, for they serve also to reduce interspecific competition.

Movement into a special microhabitat, at the time of courtship and mating, is probably more common than published observations would suggest, not only among snakes but also among other vertebrate groups. Many animals are commonly encountered in the field, yet are almost never seen engaged in reproductive activities. Of course, in some cases the animals may, at the time of mating, simply invade a microhabitat where they are exceptionally well concealed from predators.

Although snakes are most closely related to lizards, the two groups show no great similarity in courtship behavior. The courtship of lizards has been investigated by Noble and Bradley (1933).

Wholly sterile hybrids have not been observed in snakes. Hybrids between the red ratsnake and the Everglades ratsnake exhibit marked hybrid vigor.

Occasional hybridization, producing adaptively inferior hybrids, is not necessarily dysgenic, for it results in selection for greater isolation; and there is at least a possibility that the new genotype could exploit some abrupt change in the environment (Epling, 1947).

SUMMARY

Isolating mechanisms have been listed in a variety of arrangements (e.g., Dobzhansky, 1951; Mayr, 1942). The present arrangement (Table 1), based upon the snakes, is useful in that the various mechanisms may be thought of as operative in sequence. Thus, if two congeneric species are separated geographically, they cannot interbreed; if they are not so separated, they may yet be isolated by restriction to different habitats; if frequenting the same habitat, they may still be separated by invasion of different microhabitats in the mating season; and so on down the list. This arrangement also permits grouping into extrinsic vs. intrinsic mechanisms, and into pre-mating vs. post-mating ones.

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